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Reflexive and Preparatory Selection and Suppression of Salient Information in the Right and Left Posterior Parietal Cortex

Carmel Mevorach¹, Glyn W. Humphreys¹, and Lilach Shalev²

Abstract

■ Attentional cues can trigger activity in the parietal cortex in anticipation of visual displays, and this activity may, in turn, induce changes in other areas of the visual cortex, hence, implementing attentional selection. In a recent TMS study [Mevorach, C., Humphreys, G. W., & Shalev, L. Opposite biases in salience-based selection for the left and right posterior parietal cortex. *Nature Neuroscience*, 9, 740–742, 2006b], it was shown that the posterior parietal cortex (PPC) can utilize the relative saliency (a nonspatial property) of a target and a distractor to bias visual selection. Furthermore, selection was lateralized so that the right PPC is engaged when salient information must be selected and the left PPC when the salient information must be ignored. However, it is not clear how the PPC implements these

complementary forms of selection. Here we used on-line triple-pulse TMS over the right or left PPC prior to or after the onset of global/local displays. When delivered after the onset of the display, TMS to the right PPC disrupted the selection of the more salient aspect of the hierarchical letter. In contrast, left PPC TMS delivered prior to the onset of the stimulus disrupted responses to the lower saliency stimulus. These findings suggest that selection and suppression of saliency, rather than being “two sides of the same coin,” are fundamentally different processes. Selection of saliency seems to operate reflexively, whereas suppression of saliency relies on a preparatory phase that “sets up” the system in order to effectively ignore saliency. ■

INTRODUCTION

In everyday life, the brain is bombarded with more visual information than we can act on at any one time. Efficient behavior, then, relies on a process of attentional selection which is required to filter out irrelevant stimuli and to prioritize behaviorally relevant events. Importantly, this attentional prioritization process needs to be flexible in order to be responsive to the changing demands of different environments and tasks.

In recent years, a growing number of imaging studies have looked at the functional relevance of the parietal cortex in modulating attentional selection (see Corbetta & Shulman, 2002; Kanwisher & Wojciulik, 2000 for reviews). Specifically, several studies have focused on dissociating preparatory processes following an attentional cue or task instruction from the visual analysis of subsequent signals (e.g., Corbetta, Kincade, & Shulman, 2002; Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Hopfinger, Buonocore, & Mangun, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Shulman et al., 1999). Kastner et al. (1999) first demonstrated that attention preparation could modulate activity in the retino-

topic cortex even in the absence of visual stimulation—generating a form of baseline shift on subsequent visual processing. It was also shown that this baseline shift was strong in parietal and frontal areas and, critically, activation in these areas did not differ according to the presence or absence of the visual target. Other studies (e.g., Corbetta et al., 2000, 2002) have replicated these results while also showing that the temporo-parietal cortex responds to a cue alone, when cue-only trials are included in the protocol. Together, these data provide support for the hypothesis that a fronto-parietal network is responsible for top-down spatial attention (preparatory) signals that modulate activity elsewhere in the visual system.

Whereas Kastner et al.'s (1999) study was concerned with spatial expectancies for targets, other studies have found that fronto-parietal activation is linked to forms of nonspatial attentional selection including selection by color and shape (Le, Pardo, & Hu, 1998), temporal interval (Coull, Frith, Büchel, & Nobre, 2000), motion (Shulman et al., 1999), and stimulus category (e.g., faces vs. houses; O'Craven, Downing, & Kanwisher, 1999). Notably, nonspatial attention, like spatial attention, can affect visual processing in a preparatory manner with, in this case, increased activation occurring in specialized visual areas (e.g., fusiform face area or parahippocampal place area [PPA] for faces and houses) when a cue directs attention to

¹University of Birmingham, Edgbaston, Birmingham, UK, ²Hebrew University, Mount Scopus, Jerusalem, Israel

a face or a house prior to the onset of the visual display (Serences, Schwarzbach, Courtney, Golay, & Yantis, 2004).

Although wide areas of the parietal cortex show a response to increases in attentional demands (e.g., Wojciulik & Kanwisher, 1999), there is some evidence for functional segmentation within this region. Coull and Nobre (1998), for instance, found that temporal selection was linked to activation of the left inferior parietal lobule (IPL), whereas spatial shifts of attention were associated with superior parietal lobule (SPL) activity. Wojciulik and Kanwisher (1999) have also associated SPL and IPL activity to spatial and nonspatial selection, respectively. Whether these different brain regions are *necessarily* involved in different forms of selection can be tested by using intervention procedures such as transcranial magnetic stimulation (TMS). TMS can temporarily alter activity within a given brain region, enabling the effects of local changes in activation to be mapped behaviorally. In one example study, Chambers, Payne, Stokes, and Mattingley (2004) found that stimulation of the right IPL (specifically the angular gyrus [AG]) affected spatial orienting, whereas stimulating either the left AG or the supramarginal gyrus (SMG) in either hemisphere did not affect performance. Rushworth, Ellison, and Walsh (2001) have even reported a double dissociation between the effects of stimulation over the right IPS/IPL and over the left anterior IPS on, respectively, spatial attention (specifically on the ability to reorient attention after an invalid cue) and attention toward motor planning and preparation. These data are consistent with the proposal that contrasting regions within the posterior parietal cortex (PPC) may modulate processing according to the nature of the underlying selection process.

In a series of recent studies, we have demonstrated an additional lateralization in the PPC of another form of nonspatial attentional selection—where stimuli are selected on the basis of their relative salience.¹ Using variants of the classic global/local task (Navon, 1977), we orthogonally manipulated the level of shape that participants responded to and the salience of that information. For example, the local items had high salience when contrast differences were introduced between the local elements, whereas the global shape was salient when the overall stimulus was blurred (see also Lamb & Robertson, 1988). Note that in the global/local task, the global shape cannot be attended spatially without the local elements also falling within the same “attentional window,” hence, the task examines a form of nonspatial selection (cf. Heinke & Humphreys, 2003). In an initial study, patients with left parietal damage were highly susceptible to interference from the more salient level of the stimulus, irrespective of whether this was at the global or local level (Mevorach, Humphreys, & Shalev, 2006a). The evidence indicates that the left PPC was involved in selecting low salient stimuli, not, as previously thought, in directing attention to local elements. Con-

verging evidence came from a study using repetitive TMS (rTMS) over the left and right PPC of healthy participants (Mevorach, Humphreys, & Shalev, 2006b). rTMS over the left PPC made it harder to respond to the less salient level of global/local stimuli and to ignore information on the more salient level. In contrast, rTMS over the right PPC made it harder to select the more salient level and to ignore the less salient level. This result occurred irrespective of whether the local or global stimuli were the most salient. In a recent fMRI study (Mevorach, Shalev, Allen, & Humphreys, *in press*), we have furthermore demonstrated activation along the left intraparietal sulcus (IPS), including regions in the left AG and the left SMG, when low salient stimuli were selected.

How such a lateralized network of salience-based selection is implemented at a functional level is still an open question. One conjecture is that both the right and left PPC modulate the effects of salience in a top-down preparatory fashion consistent with these areas being involved in the production of a preparatory attentional signal (e.g., Kastner et al., 1999). For example, it may be that the right PPC provides an enhancement signal for “pure” bottom-up salience computed in the visual cortex, whereas the left PPC provides an attenuation signal for such visual areas. Thus, both left and right PPC induce a “baseline shift” in the visual cortex but in different directions. Another possibility is that the right PPC is responsible for detecting saliency in a more bottom-up fashion (Corbetta & Shulman, 2002), with responses being triggered merely by the occurrence of a salient event. The left PPC, on the other hand, can then be important for a sort of response inhibition or selection process which becomes increasingly demanding when low salience information competes with high salience information for the response (cf. Bunge, Hazeltine, Scanlon, Rosen, & Gabrieli, 2002).

One way of exploring these possibilities is to examine the critical temporal parameters that determine the involvement of the left and right PPC in salience-based selection. For example, if the left and right PPC are primarily engaged in producing preparatory enhancement or attenuation signals, we would expect both regions to be engaged in the period of time preceding the onset of the visual stimuli. On the other hand, if the right PPC is important for bottom-up responses to salient stimuli, we would expect it to be crucial only after visual targets are presented. Similarly, if the left PPC is important for response selection (or inhibition), we would expect it to be critical only after the visual information has been processed. Here we test these alternatives by using on-line triple-pulse rTMS over the PPC either immediately before the onset of a global/local letter or following its offset while subjects are asked to identify either the global or the local aspects. A variety of TMS studies have now demonstrated that on-line processing of stimuli can be disrupted by TMS presented after a target has

appeared (e.g., Ellison & Cowey, 2007; Ashbridge, Walsh, & Cowey, 1997). In Experiment 1, stimulation was given over the right PPC. We ask whether the right PPC modulates the selection of high saliency targets in a preparatory or a reflexive manner. In Experiment 2, stimulation was applied over the left PPC. Here we evaluated whether the left PPC operates in a preparatory or reflexive manner to bias selection to targets that are behaviorally relevant but low in saliency. As in our previous studies, the saliency of the local and global levels of a stimulus was manipulated orthogonally with the level of the target so that we were able to compare the effect of on-line TMS on selection based on saliency across different hierarchical levels. In our previous TMS study (Mevorach et al., 2006b), we have used P3 and P4 on the 10–20 EEG coordinate system to guide localization of the TMS coil. As we have shown there, these locations corresponded, on average, to the banks of the left and right posterior IPS, respectively. We used the same methodology here to guide positioning of the TMS coil.

EXPERIMENT 1: THE CRITICAL TIME WINDOW FOR THE RIGHT PPC

Methods

Participants

Twelve healthy right-handed participants drawn from the local student population at the University of Birmingham gave written informed consent to participate in the study and were naïve to its purpose. The study was conducted in accordance with the Declaration of Helsinki and the methodology had been approved by the local ethics committee.

Transcranial Magnetic Stimulation

A 70-mm figure-of-eight coil connected to a MagStim Rapid stimulator (MagStim, Whitland, UK) was positioned over the right PPC (P4 on the 10–20 EEG coordinate system). The coil was kept tangential to the head with the handle pointed posteriorly. Each trial consisted of triplets of TMS pulses presented at a frequency of 20 Hz and at 60% of the stimulator's maximum output. Intensity was not decided according to motor threshold (or any other individual index). Previously, it has been shown that motor thresholds are not necessarily a good indication for visual cortex excitability (Stewart, Walsh, & Rothwell, 2001). The stimulation level was selected on the basis of previous studies which have shown the level to be sufficient to disrupt cortical functions in sensory and association cortices. Two possible conditions of stimulation were used. In one condition (pre-onset), rTMS was given 150 msec prior to the onset of the hierarchical letter target (with the last pulse given 50 msec prior to the onset of the target), and in the other condition (post-offset), rTMS was given 50 msec following

the offset of the visual display (i.e., the first pulse was given 150 msec following the onset of visual display and the last pulse 250 msec following the target onset; see Figure 1B). The rTMS train frequency, intensity, and duration were well within safe limits (Wassermann, 1998).

Stimuli

The stimuli were presented on a 17-in. monitor (1024×768 pixels) of a Gateway PC. The viewing distance was approximately 60 cm so that each centimeter on the screen represented 0.96° of visual angle. All the stimuli appeared against a black background. Two sets of displays were used to represent high global saliency and high local saliency. For the condition with relatively high local saliency, the compound stimuli were created from orthogonal combinations of the letters H and S. Each compound contained both red and white local letters (see Figure 1A). Each local letter subtended $1.34^\circ \times 1.06^\circ$ of visual angle (in width and height, respectively) and the global letter subtended $8.26^\circ \times 5.38^\circ$ of visual angle (in width and height, respectively). The interelement distance was 0.38° . In the condition with relatively high global saliency, the compound letters were again composed of the letters H and S, which were combined orthogonally at the local and global levels. All the local letters were red. Each local letter subtended $1.34^\circ \times 1.06^\circ$ of visual angle (in width and height, respectively) and the global letter subtended $5.66^\circ \times 4.51^\circ$ of visual

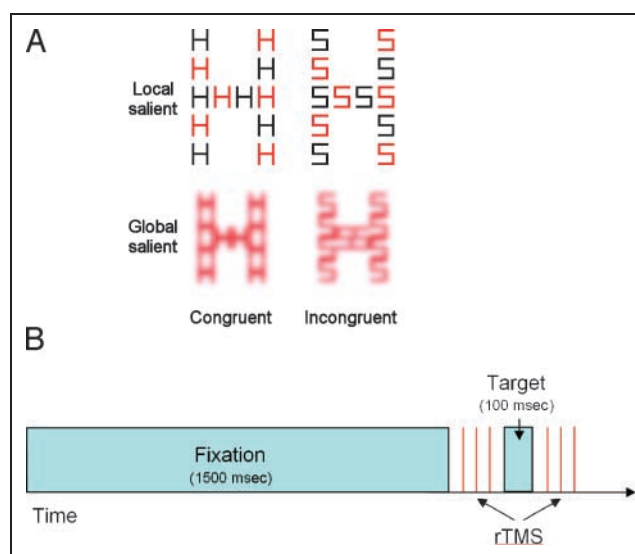


Figure 1. Example of stimuli and procedure for the global/local task. (A) Two display sets were used to achieve local saliency (upper pair) and global saliency (lower pair). The compound letters are displayed here on a white background, whereas in the actual experiment we used a black background. (B) Each trial began with a fixation cross which was displayed for 1500 msec. Two hundred milliseconds following the offset of the fixation, the target hierarchical letter appeared for 100 msec. In different trials, three TMS pulses 50 msec apart (denoted by the red lines) were given starting either 150 msec before target onset or 50 msec following target offset.

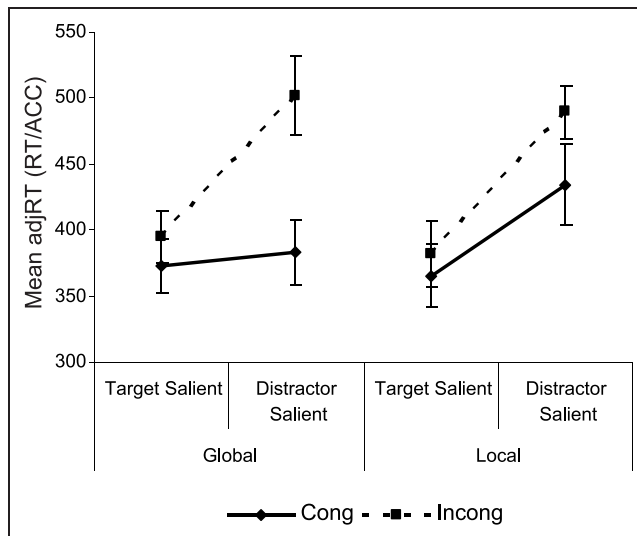


Figure 2. Performance in the global/local task in the training/baseline condition (Experiment 1). Mean adjRTs (\pm SEM) for the global and local letter identification as a function of target saliency (target-salient and distractor-salient).

angle (in width and height, respectively). The distance between local elements was 0.96° . These letters underwent a blur procedure in Paint Shop Pro 7.0 with factor = 7. The compound letters could appear at one of two possible locations at 1.3° above or below fixation along the vertical midline, which was done to ensure that participants performed the task under conditions encouraging diffuse attention (cf. Grice, Canham, & Boroughs, 1983). A white cross (0.57°) served as fixation and was presented in the center of the screen.

Experimental Procedure

On different blocks of 40 trials, participants were asked to identify the global or the local elements of the compound letter while ignoring information on the other level. On half of the trials, the compound figures consisted of the same global and local elements (congruent trials), and on the other half there were different global and local elements (incongruent trials). Each trial began with the presentation of a fixation cross for 1500 msec. Following a 200-msec interval, the target compound letter appeared for 100 msec. Participants were required to make a speeded response to the identity of the letter on the target level (H or S) by pressing one of two keyboard keys ("k" and "l") using their right hand. Following the keypress, the next trial began. In addition, a sequence of three TMS pulses (50 msec apart) was given either 150 msec before the onset of the target compound letter or 50 msec following its offset. The order of the stimulation times was randomized. Each run of the task included four blocks (two with "global" targets and two with "local" targets). A written instruction ("global task" or "local task") appeared at the center of

the screen 2 sec prior to the beginning of each block. The first two blocks and the last two blocks of each run were both either with the global target being more salient or with the local target being more salient (the order was counterbalanced across subjects and runs). Each participant completed three runs: The first run served as a training/baseline procedure during which no TMS was applied. This was then followed by two consecutive TMS runs. To prevent overheating, the TMS coil was replaced between the second and third runs of the task.

Data Analysis

In order to incorporate both RT and accuracy in a single measure, we used RT/proportion correct as our dependent measure (the adjusted reaction times [adjRT]; Townsend & Ashby, 1983; see also Mevorach et al., 2006b; Chambers et al., 2004, for recent uses of such a measure in the context of TMS which can increase both RTs and errors). In the present case, some participants had a high rate of errors ($>10\%$) in certain conditions, making it difficult to assess RTs alone.

Results and Discussion

Training/Baseline

Participants' adjRTs for the training/baseline run are plotted in Figure 2. A repeated measures ANOVA was carried out on participants' adjRTs with saliency (target-salient vs. distractor-salient²), target level (global vs. local), and congruency (congruent vs. incongruent) as within-subject factors. Participants were better at identifying the target level when it was salient (379 msec/proportion correct) than when the distractor level was more salient [452 msec/proportion correct; $F(1, 11) = 70.238$, $p < .001$] and congruent displays were identified faster than incongruent ones [389 and 442 msec/proportion correct, respectively; $F(1, 11) = 35.027$, $p < .001$]. Furthermore, a significant interaction of saliency and congruency [$F(1, 11) = 11.484$, $p < .01$] indicated that the congruency effect (adjRT incongruent – adjRT congruent) was smaller when the target level was more salient compared with when the distractor level was more salient (19 and 87 msec/proportion correct for target-salient and distractor-salient, respectively). However, a marginally significant three-way interaction of saliency, level, and congruency [$F(1, 11) = 3.397$, $p = .092$; see Figure 2] suggested that the change in congruency effect according to target saliency was more pronounced for identifying the global level target (22 and 119 msec/proportion correct for target-salient and distractor-salient stimuli, respectively) than the local level target (16 and 55 msec/proportion correct for target-salient and distractor-salient stimuli, respectively). These data confirm that the relative saliency was reversed for the two different saliency conditions (albeit

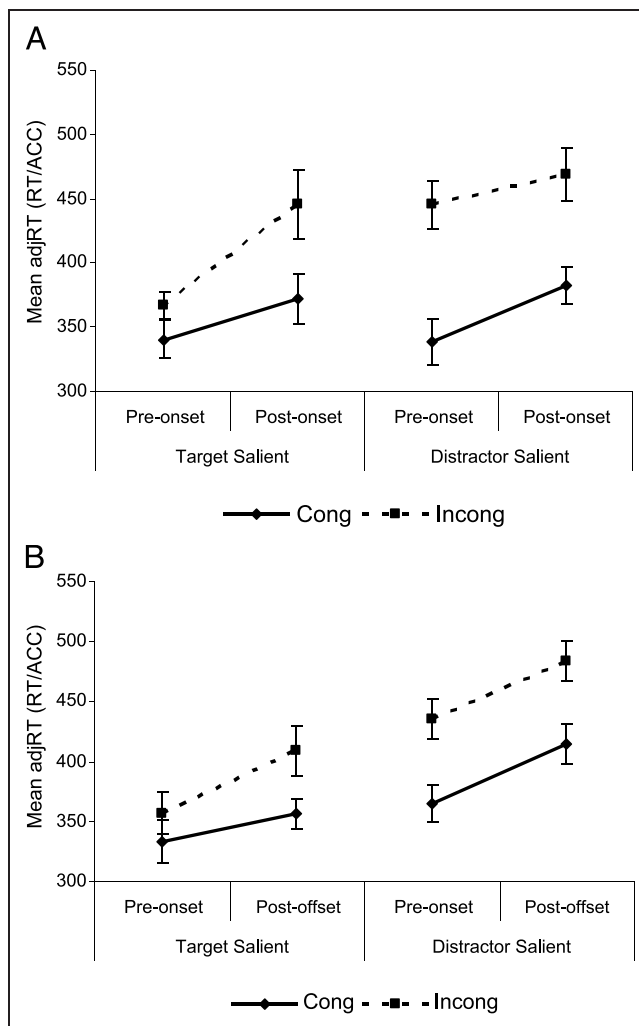


Figure 3. Performance in the global/local task following rTMS over the right PPC. (A) Mean adjRTs (\pm SEM) for global identification under pre-onset and post-onset rTMS. (B) Mean adjRTs (\pm SEM) for local identification under pre-onset and post-onset rTMS.

not symmetrically, so that the saliency manipulation was stronger for the global task). The results also fit with our previous findings using a slightly different version of the current paradigm (e.g., Mevorach et al., 2006b).

TMS Effects

In order to assess the critical time window in which the right PPC is involved in selection by saliency, a repeated measures ANOVA was carried out on participants' adjRTs for the TMS run of the task with the factors being TMS time (pre-onset vs. post-onset), saliency (target-salient vs. distractor-salient), level (global vs. local), and congruency (congruent vs. incongruent) (see Figure 3). A main effect of TMS time indicated that responses were overall quicker for the pre-onset condition (373 msec/proportion correct) than for the post-onset condition [417 msec/proportion correct; $F(1, 11) = 32.88, p < .001$]. Per-

formance was also better when the target level was more salient than the distractor level [372 and 417 msec/proportion correct for the target-salient and distractor-salient conditions, respectively; $F(1, 11) = 26.317, p < .001$], and performance was better with congruent displays (363 msec/proportion correct) than with incongruent ones [427 msec/proportion correct; $F(1, 11) = 92.246, p < .001$]. Performance did not differ, however, for the global (395 msec/proportion correct) and local (394 msec/proportion correct) tasks [$F(1, 11) < 1$]. A further interaction of saliency and level [$F(1, 11) = 10.513, p < .005$] indicated that the effect of saliency on overall performance (i.e., regardless of congruency) was more pronounced in the local task (364 and 425 msec/proportion correct for target and distractor salient, respectively) than in the global task (382 and 408 msec/proportion correct for target and distractor salient, respectively). Most importantly, a three-way interaction of TMS time, saliency, and congruency emerged [$F(1, 11) = 5.765, p < .05$]. There were differential effects of stimulating the right PPC prior to or immediately after displaying the hierarchical letter (Figure 3). Planned comparisons indicated that, for the target-salient condition, rTMS applied post-onset resulted in a larger congruency effect (87 msec/proportion correct) than rTMS applied pre-onset [25 msec/proportion correct; $t(11) = 2.807, p < .01$]. However, for the distractor-salient condition, there was no difference in the congruency effects that occurred with pre-onset or post-onset rTMS [89 and 78 msec/proportion correct, respectively; $t(11) = 0.950, ns$; Figure 4].

The finding that pre-onset rTMS resulted in more efficient performance compared with post-onset rTMS might be expected given the audible features of TMS.

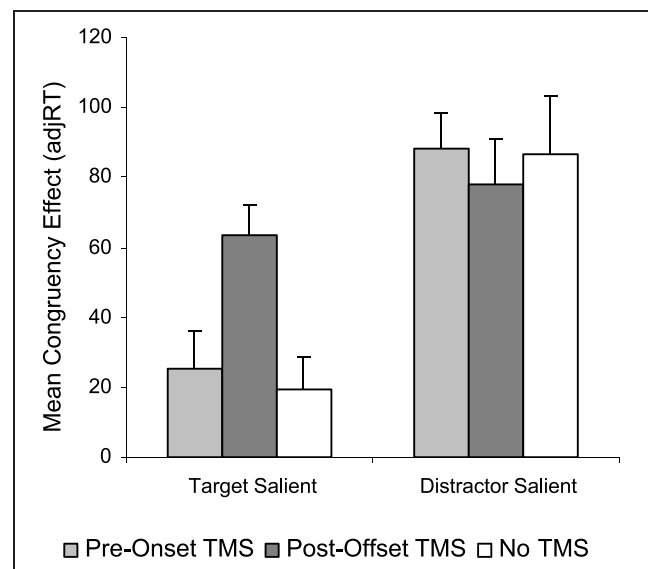


Figure 4. Mean congruency effects (incongruent adjRT – congruent adjRT) (\pm SEM) for target-salient and distractor-salient conditions according to time of rTMS over the right PPC. The data are pulled across the different hierarchical levels.

The sound emitted from the stimulator may have alerted participants for the occurrence of the hierarchical letter, which resulted in a speeded response. However, the interaction of TMS time, saliency, and congruency suggests that, on top of any general effects, post-offset TMS time had a differential effect as a function of the saliency of the target level and the congruency of the display. This interaction fits with the argument that the right PPC responds to high saliency stimuli in a reflexive manner, following the occurrence of the stimulus (see also Mevorach et al., 2006b). TMS over the right PPC had an increased effect on conditions in which the target level was more salient than the distractor level (i.e., when salient information had to be selected in competition with less salient distracting information), compared with when less salient information had to be selected (in the distractor-salient condition). Moreover, this was most evident when stimulating the PPC after the visual information was available for processing (in the post-offset condition). We discuss these points further in the General Discussion. We now turn to evaluating the critical time frame for the involvement of the left PPC in salience-based selection.

EXPERIMENT 2: THE CRITICAL TIME WINDOW FOR THE LEFT PPC

Methods

Participants

Twelve healthy right-handed participants drawn from the local student population at the University of Birmingham gave written informed consent to participate in the study and were naïve to its purpose. One participant had to be withdrawn from the analysis as in one of the conditions he completely failed to respond correctly (0% accuracy). The study was conducted in accordance with the Declaration of Helsinki and the methodology had been approved by the local ethics committee.

Stimuli and Procedure

The stimuli and procedure for Experiment 2 were identical to those of Experiment 1 apart from the stimulation site for rTMS which was over the left PPC (P3 on the 10–20 EEG coordinate system). As in Experiment 1, participants initially performed one run of the global/local task without TMS, which was then followed by two runs during which on-line rTMS was applied.

Results and Discussion

Training/Baseline

The mean performance across participants in the training/baseline run is plotted in Figure 5. A repeated measures ANOVA was carried out on the adjRT measure with saliency (target-salient vs. distractor-salient), target level

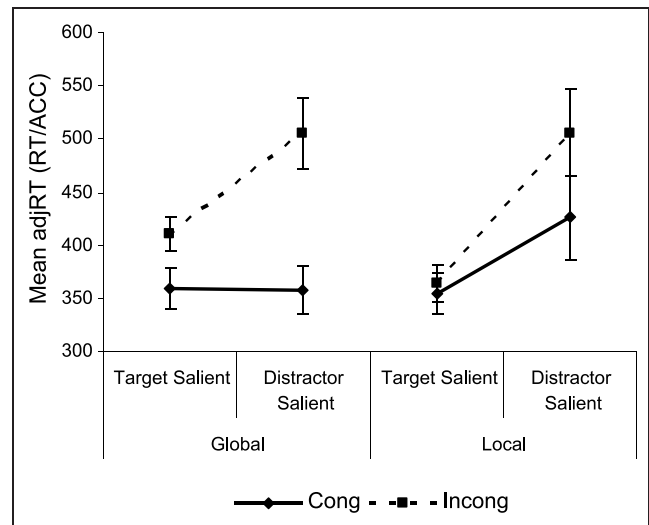


Figure 5. Performance in the global/local task in the training/baseline condition (Experiment 2). Mean adjRTs (\pm SEM) for the global and local letter identification as a function of target saliency (target-salient and distractor-salient).

(global vs. local), and congruency (congruent vs. incongruent) as within-subject factors. Participants were better at identifying the target level when it was salient (373 msec/proportion correct) than when the distractor level was more salient [449 msec/proportion correct; $F(1, 10) = 14.730$, $p < .005$], and congruent displays were identified faster than incongruent ones [375 and 447 msec/proportion correct for congruent and incongruent displays, respectively; $F(1, 10) = 41.256$, $p < .001$]. There was a significant interaction between saliency and congruency [$F(1, 10) = 24.379$, $p < .001$], indicating that the congruency effect for the target-salient condition (32 msec/proportion correct) was smaller than for the distractor-salient condition (114 msec/proportion correct). In addition, there was a borderline interaction between level and congruency [$F(1, 10) = 4.568$, $p = .058$], indicating a tendency for the congruency effect to be larger for the global identification task (99 msec/proportion correct) than for the local identification task (45 msec/proportion correct). However, this held irrespective of the saliency conditions. It might be the case that the particular way in which relative saliency was manipulated in the two displays was not fully symmetrical (i.e., effects found for the global and local tasks may not be identical). However, similarly to Experiment 1, these data still confirm that relative saliency was reversed for the two different saliency conditions, whereas global identification tended to show larger congruency effects generally.

TMS Effects

The mean performance for the TMS runs of the task is plotted in Figure 6. In order to assess the critical time window in which the left PPC is involved, a repeated

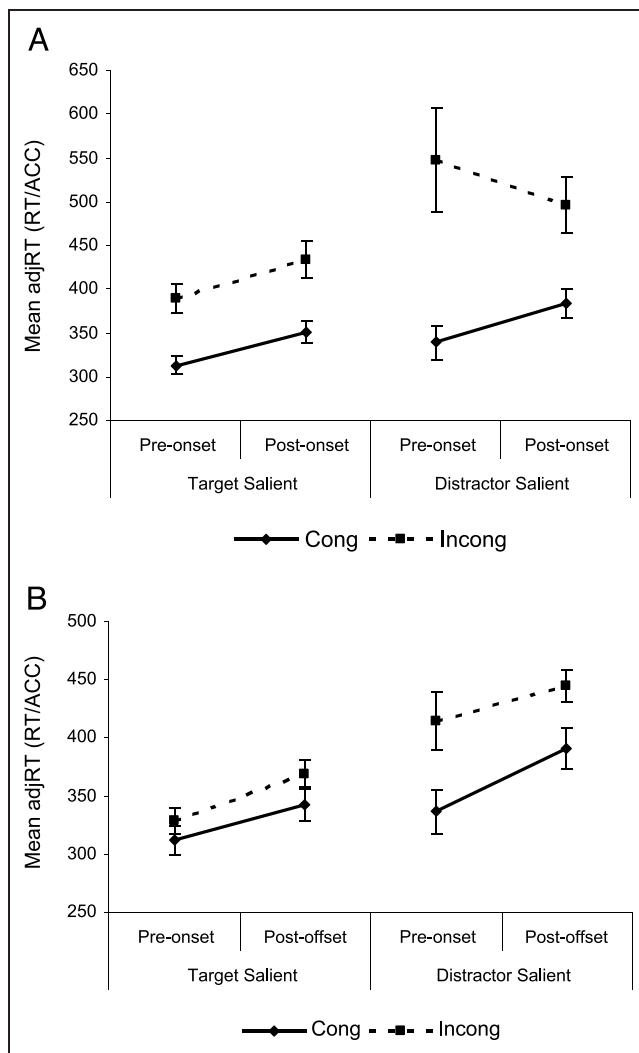


Figure 6. Performance in the global/local task following rTMS over the left PPC. (A) Mean adjRTs (\pm SEM) for global identification under pre-onset and post-onset rTMS. (B) Mean adjRTs (\pm SEM) for local identification under pre-onset and post-onset rTMS.

measures ANOVA was carried out on participants' adjRT with the within-subjects factors being TMS time (pre-onset vs. post-onset), saliency (target-salient vs. distractor-salient), level (global vs. local), and congruency (congruent vs. incongruent). A main effect of TMS time indicated that responses were quicker for the pre-onset condition [373 msec/proportion correct] than the post-onset condition [402 msec/proportion correct; $F(1, 10) = 14.862$, $p < .005$]. As noted above, this main effect is expected given the "alerting" effects of stimulating before compared with after the onset of a display. Performance was better (i) when the target level was more salient than when the distractor level was more salient [355 and 419 msec/proportion correct for the target-salient and distractor-salient conditions, respectively; $F(1, 10) = 18.042$, $p < .005$], (ii) in the local identification task (367 msec/proportion correct) compared with the global

identification task [407 msec/proportion correct; $F(1, 10) = 8.089$, $p < .05$], and (iii) with congruent displays (346 msec/proportion correct) compared with incongruent displays [428 msec/proportion correct; $F(1, 10) = 47.980$, $p < .001$]. In addition (and similar to the baseline condition), an interaction between level and congruency [$F(1, 10) = 10.026$, $p < .01$] revealed that the congruency effect was larger for the global identification task (120 msec/proportion correct) than for the local identification task (43 msec/proportion correct). Most importantly, there was once again a three-way interaction of TMS time, saliency, and congruency [$F(1, 10) = 6.983$, $p < .05$], revealing that there were differential effects of stimulating the left PPC prior to or immediately after displaying the hierarchical letter (Figure 6). Planned comparisons indicated that the congruency effect for the distractor-salient condition was substantially larger following pre-onset rTMS than it was after post-onset rTMS [143 and 83 msec/proportion correct, respectively; $t(10) = 2.367$, $p < .05$]. However, this time there was no difference in the congruency effects that occurred following pre-onset or post-onset rTMS with high saliency targets [47 and 54 msec/proportion, respectively; $t(10) = 0.597$, ns ; Figure 7].

These data again fit with the saliency-based account of selection proposed by Mevorach et al. (2006a, 2006b), in which the left PPC is critical for selecting targets that are relatively low in saliency compared with distractors, and this holds irrespective of whether stimuli must be selected at the local or the global level. Moreover, the data demonstrate that the role of the left PPC in selecting low saliency targets is preparatory in nature, with there being greater disruption to the selection of low saliency

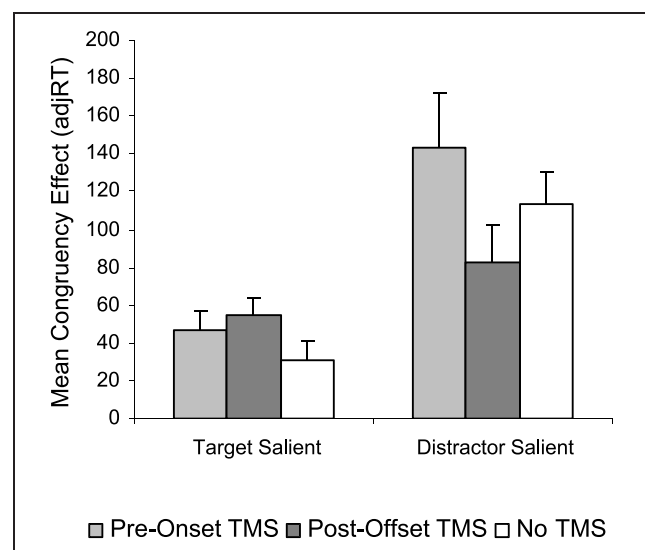


Figure 7. Mean congruency effects (incongruent adjRT – congruent adjRT) (\pm SEM) for target-salient and distractor-salient conditions according to time of rTMS over the left PPC. The data are pulled across the different hierarchical levels.

targets when rTMS was applied pre-onset than when it occurred post-offset. In contrast, there was no hint of a differential effect of the time when rTMS was applied when the target level was more salient than the distractor level (target-salient condition). In the General Discussion, we consider how this anticipatory effect may operate.

GENERAL DISCUSSION

In the present study, we looked further into the mechanisms that implement salience-based selection in the brain, focusing on the time window during which the right PPC (Experiment 1) and the left PPC (Experiment 2) are critical in achieving selection by saliency. In accord with our previous findings (Mevorach et al., 2006b), we confirmed that the right PPC is specifically linked to the selection of salient information in the face of low saliency distractors; in contrast, the left PPC is specifically involved in selecting low saliency targets in the presence of higher saliency distractors. Critically, however, the present data indicate that the right and left PPC modulate saliency-based selection across different time windows. This, in turn, suggests that the selection of high and low saliency stimuli may be achieved differently. We discuss this below.

Reflexive Selection of Salient Information

At the outset of the article, we asked whether right PPC involvement in the selection of highly salient information is linked to preparatory processes that “set up” the attentional system to be ready for salient events, or to a reflexive process triggered by the occurrence of a salient event. We suggested that rTMS given prior to the onset of the stimulus would tend to disrupt preparatory activity while any reflexive responding to the stimuli would be more disrupted by poststimulus rTMS. The present evidence indicates a poststimulus effect of rTMS to the right PPC because rTMS at that time maximally disrupted the selection of the high saliency target while having minimal effect on the selection of the low saliency target. This is consistent with the right PPC being involved in reflexive responding to high saliency events. It is important to note here that we have manipulated several stimulus parameters to effectively change the relative saliency of the global and local levels of form. However, the effects we obtain hold across the different levels and across the different stimulus parameters. Thus, these effects reflect sensitivity to relative saliency per se, rather than sensitivity to a specific display parameter (such as size or interitem distance).

Although previous investigations have revealed parietal involvement both in preparing for an event to occur and in response to the event (see Corbetta & Shulman, 2002 for a review), there is evidence for a right-localized

ventral fronto-parietal network in reflexive orienting to a salient or unexpected event. For instance, Corbetta et al. (2000) used the classic Posner (1980) paradigm with endogenous cues to compare activation elicited by the cue with that associated with the appearance of the target (especially on invalid trials). They found that the SPL (bilaterally) was implicated in preparatory processes maintaining attention toward a location in the visual field prior to the onset of a target, whereas the right temporal-parietal junction (TPJ) was more active when a target appeared in an unexpected location. This can be interpreted as the right PPC specifically responding to the onset of a stimulus, even when it is unexpected. This also fits with data from the neurological syndrome of unilateral visual neglect, classically associated with damage to the right PPC (Mort et al., 2003, although see Karnath, Ferber, & Himmelbach, 2001). Patients with visual neglect are able to endogenously orient attention to their contralesional side, but are impaired at detecting targets when cued to the ipsilesional field (Riddoch & Humphreys, 1983; see also Posner, Walker, Friedrich, & Rafal, 1984). Riddoch and Humphreys (1983) suggested that this reflected impairments to a system that pulled attention reflexively to contralesional targets. The present results provide converging evidence in which TMS to the right PPC, delivered after the stimulus, selectively disrupts reflexive responses to high saliency targets. A number of previous TMS studies have found effects of right parietal stimulation on spatial attention. However, those studies have mainly focused on conditions in which spatial attention must move serially in the visual field (such as in conjunctive search conditions; e.g., Ashbridge et al., 1997), must reorient attention following an invalid spatial cue (such as in the Posner spatial cueing paradigm; e.g., Chambers et al., 2004), or must orient attention to two different locations (left and right) simultaneously (such as in a spatial extinction paradigm; e.g., Hilgetag, Théoret, & Pascual-Leone, 2001). One interesting point here though is that these processes were absent in our task. Indeed, our effects are unlikely to reflect selecting a single location of space as we used centrally presented hierarchical stimuli in which the global forms could not be attended spatially without attention also being allocated to the local elements. An alternative is that the right PPC is involved not only in allocating attention to one location in space (if you like, in moving a spotlight of visual attention across the scene) but also in allocating attention to the appropriate area (and perhaps, also scale) (altering the spread and focus of attention). Critically, we propose that this directing of attention to a given spatial area is determined by the bottom-up saliency of the stimulus. Indeed, we found no differential effect on the selection of the high saliency target from rTMS delivered prior to the onset of the target. This suggests that participants may not have engaged in anticipatory setting of attention when they knew in advance that the target is the more salient aspect of the display.

Although our data indicate effects on aspects of the spread of attention and not just on shifts of any attentional spotlight, we should note that the area we have stimulated (P4 on the 10–20 EEG coordinate system) most likely targets IPS/IPL rather than the TPJ (see Mevorach et al., 2006b for confirmatory evidence). It may be, then, that different regions of the right PPC support different aspects of saliency-based selection (e.g., with the TPJ supporting selection of salient locations and the IPS/IPL supporting selection of saliency of form). This would fit with the notion that functional segmentation exist in the parietal cortex (e.g., Rushworth et al., 2001; Wojciulik & Kanwisher, 1999; Coull & Nobre, 1998), but needs to be investigated in future research.

Preparatory Processes for Selecting Low Saliency Targets

In contrast to the right PPC, the left PPC seems to be required when a low saliency target is selected in competition with higher saliency distractors (given the selective effects here; see also Mevorach et al., 2006a, 2006b). If the left PPC involvement in the suppression of saliency was also driven by the target stimulus, then we would have expected the strongest effects to emerge when TMS was applied poststimulus (as for the effects with TMS to the right PPC). However, we found the opposite (Experiment 2). When rTMS was over the left PPC, the effects on selecting low saliency targets were maximal when TMS occurred prior to rather than after the onset of the stimulus. One interpretation of this is that the left PPC is involved in “setting up” the system to ignore high saliency distractors. When the set-up process is disrupted, high saliency distractors are difficult to ignore and low saliency targets are, consequently, difficult to select.

The finding that pre-onset rTMS had a greater effect than post-offset rTMS on the ability to suppress saliency argues against the possibility that the left PPC is simply important for response selection (which becomes harder when salient information competes on-line for a response to a target stimulus). Alternatively, selection of the low saliency target may be boosted by presetting the system so that a bottom-up response to the most salient signal is not dominant. Behavioral studies with normal participants show that bottom-up responses to salient distractors can be modulated by the attentional “set” adopted by observers. For example, the effects of a singleton distractor are moderated when participants focus attention on a relevant target location (Theeuwes, Kramer, & Atchley, 2001); indeed, the distracting effects of such stimuli are maximized when observers adopt a “singleton detection” mode, and the effects are reduced when a specific target is expected (Bacon & Egeth, 1994). Here, participants may preadopt a spatial window of attention, or they may pretune target-relevant spatial frequencies (cf. Shulman & Wilson, 1987) in order to op-

timize the selection of the low saliency target. Our data indicate that this process is modulated through the left PPC.

Using single-cell recordings in monkeys, it has been shown that neurons in area LIP increase their firing rate when salient items enter their receptive field (Gottlieb, Kusunoki, & Goldberg, 1998). However, after training the monkey that the salient items are never the target, the cells’ firing rate to salient items is reduced even compared to nonsalient items (Ipata, Gee, Gottlieb, Bisley, & Goldberg, 2006). We can hypothesize that the left PPC in humans is responsible for such a baseline shift that results in a reduction of firing rate for salient but irrelevant stimuli.

Recently, we (Hodsoll, Mevorach, & Humphreys, in press) examined the effects of off-line TMS applied to either the left or right PPC on attentional capture effects from singleton distractors. Off-line TMS applied to the right PPC reduced the cost to performance from singleton distractors, supporting the argument that the right PPC modulates reflexively orienting to salience. However, TMS to the left PPC did not affect performance. In the study of singleton capture, participants did not know whether the high saliency singleton would occur on each trial, and so may not preset themselves to suppress any response to saliency. The current data indicate that the left PPC may be particularly important for establishing the preparatory state to prevent attentional capture by salient signals, and so this brain region may not be recruited when a set against saliency is not adopted.

Conclusion

The data indicate that the left PPC moderates the selection of low saliency targets presented along with higher saliency distractors, and it appears to do this by presetting the visual system not to respond to saliency. The right PPC modulates the selection of high saliency signals and appears to do so in a reflexive, on-line fashion, driven by the sensory stimulus. We suggest that the selection of high and low saliency stimuli is dependent on different brain regions that play contrasting functional roles and that operate over different time courses.

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Reprint requests should be sent to Carmel Mevorach, Behavioural Brain Sciences Centre, School of Psychology, The University of Birmingham, Edgbaston, Birmingham, B31 2DF, UK, or via e-mail: c.mevorach@bham.ac.uk.

Notes

1. Saliency was defined operationally as a difference in performance. That is, highly salient information is expected to be processed more quickly and accurately than information

low in salience and to exert greater interference over low saliency information than vice versa. Note, however, that the particular stimuli parameters that invoke such differences in saliency are not in the focus of this work.

2. The target-salient condition includes the global-salient blocks, in which the global level was the target, and the local-salient blocks, in which the local level was the target. Similarly, the distractor-salient condition includes the global-salient blocks, in which the local level was the target, and the local-salient blocks, in which the global level was the target.

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